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Estimating the compensation irradiance in the ocean: The importance of accounting for non-photosynthetic uptake of inorganic carbon

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ABSTRACT

The compensation irradiance, the irradiance at which net photosynthesis is zero over a 24-h period, was estimated at station ALOHA (22°45′N, 158°W) from analysis of ^{14}C uptake rates measured from 8 January 1989 to 13 June 1990 at depths ranging from 5 to 175 m. The estimates were made on the basis of linear regressions of the difference between light bottle and dark bottle ^{14}C uptake in the light-limited region of the euphotic zone and determination of the depth at which the difference between the uptake rates was zero. About half of the non-photosynthetic ^{14}C uptake at the compensation irradiance could be attributed to chemolithoautotrophy; the remainder was presumably due to anaplerotic processes. Deriving the compensation irradiance by extrapolating dawn-to-dawn light-bottle uptake above the compensation irradiance to zero resulted in underestimation of the compensation irradiance by a factor of 2. We estimated the compensation irradiance at station ALOHA to be 0.054 mol-photons m^{-2} d^{-1}, about 0.11% of surface 400–700 nm radiation and 1% of surface 475-nm (blue) light.

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1. Introduction

In oceanography the compensation depth is defined as the depth in the water column at which net photosynthesis is zero over the course of one day (Falkowski and Raven, 2007). For many years it has been customary to assume that the compensation depth corresponds to the depth at which photosynthetically active radiation (400–700 nm light) is reduced to 1% of its value at the surface. However, as noted by Falkowski and Raven (2007), (p. 329), "The actual compensation depth is variable and certainly difficult to measure" (Banse, 2004; Falkowski and Owens, 1978; Platt et al., 1990; Ryther, 1954).

Since the development of the ^{14}C method to estimate photosynthetic rates in the ocean more than 60 years ago (Steemann Nielsen, 1951, 1952a, 1952b), measurements made by this method have provided much of the information on which the current understanding of photosynthetic rates in the ocean is based (Barber and Hilting, 2002). In addition, these measurements have been used to calibrate satellite-derived algorithms that are now being used to estimate marine primary production on a global scale (Behrenfeld et al., 2002). When measurements are made by the ^{14}C method, it is invariably the case that uptake of ^{14}C occurs in the absence of light, i.e., in bottles incubated in the dark. Uptake of inorganic ^{14}C in the dark clearly cannot represent the result of photosynthetic processes but instead may be attributed to anaplerotic carbon fixation and chemolithoautotrophy (Li, 1986). In the early years of the ^{14}C method the radioactivity assimilated in the organic matter in dark bottles was therefore subtracted from that in light bottles to correct for non-photosynthetic uptake of CO_2 (Steemann Nielsen, 1952b). The rationale for making this correction, however, has been questioned by several authors (Li, 1986; Morris et al., 1971). Li (1986), for example, has argued that much of the non-photosynthetic uptake of ^{14}C may be due to heterotrophic picoplankton and that the activities of heterotrophic picoplankton may be reduced in the light, the implication being that ^{14}C uptake in the dark would overestimate anaplerotic CO_2 uptake in the light. However, if the compensation point occurs where the irradiance is roughly 1% of the surface photosynthetically active radiation (PAR), it seems reasonable to postulate that non-photosynthetic uptake of ^{14}C is virtually the same in light and dark bottles at irradiances equal to or less than the compensation irradiance (I_C). In other words, it seems reasonable to assume that the reduction of the activities of heterotrophic picoplankton by light is a continuous function of irradiance, and in the limit of dim light becomes negligible. If this assumption is correct, then the compensation point occurs at the shallowest depth at which uptake of ^{14}C is the same in light and dark bottles incubated for

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one day (Letelier et al., 1996). Here we examine the implications of this assumption with the use of archived ^{14}C uptake data collected at the start of the Hawaii Ocean Time-series (HOT) program (Karl and Lukas, 1996) at station ALOHA (22°45′N, 158°W). Our hypothesis was that the failure to account for non-photosynthetic uptake of ^{14}C would lead to significant underestimation of the compensation irradiance.

2. Materials and methods

Water samples were collected on a total of 16 cruises from 8 January 1989 to 13 June 1990. The sampling and incubation protocols have previously been described by Karl et al. (1998). Briefly, water samples were collected using clean techniques (Fitzwater et al., 1982; Karl et al., 1996; Letelier et al., 1996) at sunrise, in most cases from a total of eight depths: 5, 25, 45, 75, 100, 125, 150, and 175 m. Prior to July 1989 simulated in situ incubations were carried out using an on-deck system that simulated both in situ photosynthetically active radiation (PAR) and temperature (Lohrenz et al., 1992). In situ incubations using a free-floating productivity array began in July 1989 (Karl et al., 1996; Letelier et al., 1996). Typically, three light and three dark 500-ml polycarbonate bottles were filled with seawater from each depth and spiked with ^{14}C-bicarbonate. The light bottles were incubated in situ for a total of 24 h. The dark bottle incubations were terminated after approximately 12 h. The specific activities of the dissolved inorganic carbon concentrations were determined from the total ^{14}C activity in 250-μl subsamples from the incubation bottles and measurements of dissolved inorganic carbon made by means of CO_2 coulometry (Winn et al., 1994). For the total activity measurements, β-phenylethylamine was used as an inorganic carbon trapping agent.

Following the incubations, subsamples of 100–500 ml were filtered onto 25-mm-diameter Whatman glass fiber GF/F filters. The filters were placed in liquid scintillation vials, 1 ml of 2 M HCl was added, and the vials were vented for 24 h to allow degassing of $^{14}CO_2$. An aliquot of 10 ml of Aquasol-II was added to each vial, and the vials were stored for approximately 30 days to allow for desorption of dissolved organic carbon from the filter matrix (Karl et al., 1998). The ^{14}C activities in the vials were measured on a Packard model 4640 liquid scintillation counter. The dark bottle uptake during 24 h was estimated by multiplying the uptake at the end of the dark incubation by 24 and dividing by the duration in hours (typically 12) of the dark bottle incubations.

We assumed that in the light-limited region of the euphotic zone (1) the photosynthetic rates were proportional to irradiance, and (2) the irradiance was linearly related to the logarithm of depth. To estimate the compensation depth on each cruise, we therefore plotted photosynthetic rates versus the logarithm of depth. We fitted a regression line to the linear portion of the data and estimated the compensation depth from the intercept of the regression line, i.e., the depth at which the photosynthetic rate estimated from the regression line equaled zero (Fig. 1). We estimated photosynthetic rates in two ways: (1) by subtracting the 24-h dark bottle uptake from the 24-h light bottle uptake, and (2) by ignoring the dark bottle uptake and basing the estimate entirely on the 24-h light bottle uptake.

Since the beginning of the Hawaii Ocean Time-series (HOT) program in 1988, measurements of surface PAR have been routinely made at 10-minute intervals on cruises with a LI-COR data logger (model LI-200 for the first 12 years and model LI-1000 since 2001) equipped with a Biospherical Instruments cosine collector. In

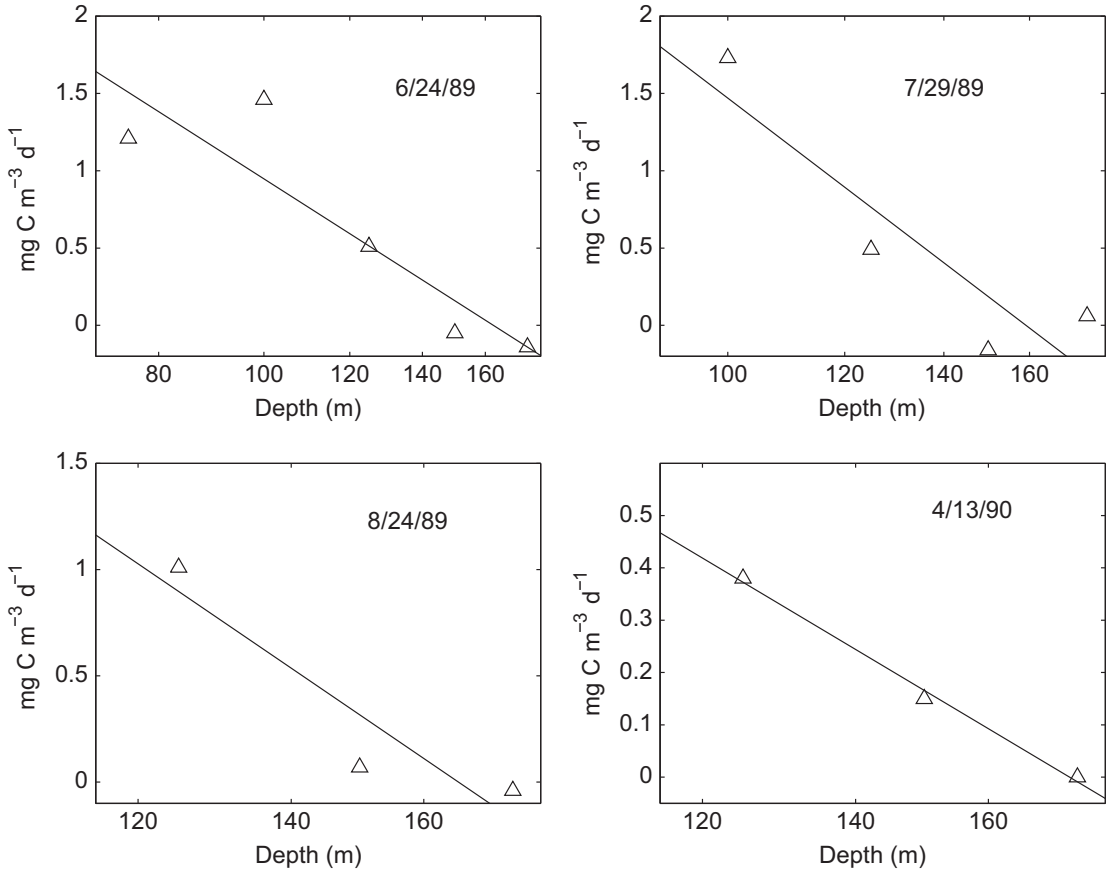


Fig. 1. Graphs of the difference between 24-h CO_2 uptake in light bottles minus dark bottles versus the logarithm of depth in the light-limited region of the euphotic zone on 4 of the 16 HOT cruises. The straight lines are model I least squares regressions fit to the data.

addition, the spectral distribution of PAR in the euphotic zone at noon on the day of the primary productivity incubations was characterized using a Biospherial Instruments profiling natural fluorescence radiometer (PNF-300) from 1990 through 1995 and a profiling reflectance radiometer (PRR-600) from 1996 through 2008; a Satlantic hyperspectral radiometer (Hyperpro-II) has been used since 2009. Because of limitations regarding the depth range of the deployment of optic profilers prior to 1998, we used data collected on HOT cruises 90 through 247 (October 2012) to model submarine PAR as a function of depth. Based on this model, we estimated the irradiances associated with the compensation depths.

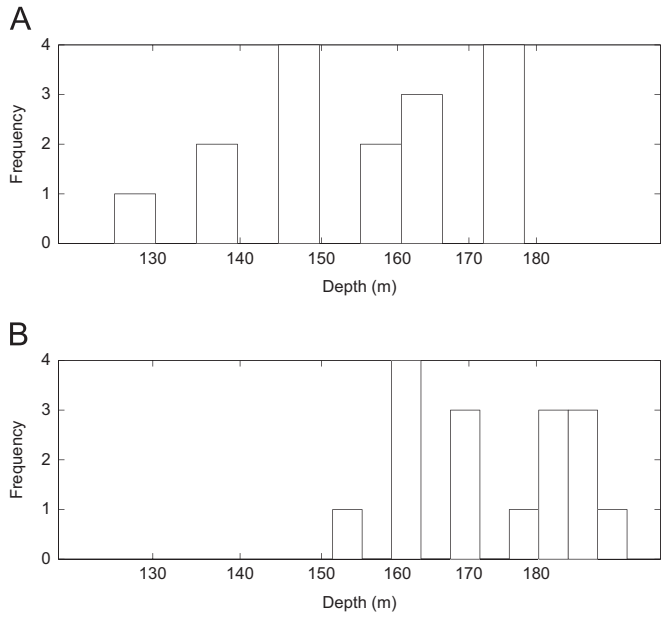


Fig. 2. Histograms of compensation depths estimated from linear regressions of (A) 24-h light bottle minus dark bottle CO_2 uptake versus the logarithm of depth and (B) 24-h light bottle uptake versus the logarithm of depth.

3. Results

Based on *t*-tests, we found no difference ($p > 0.18$) between compensation depths or compensation irradiances estimated from simulated in-situ incubations (five cruises prior to July 1989) and in-situ incubations (11 cruises beginning in July 1989). On most cruises the differences between 24-h light bottle and dark bottle CO_2 uptake at the 3 or 4 lowest depths were linearly related to the logarithm of the depths (Fig. 1). The compensation depths calculated from the 16 regression lines fit to these data were log-normally distributed (Fig. 2A). The median and geometric mean compensation depths were 159 and 155 m, respectively. Uptake of CO_2 in light bottles was also well described as a linear function of the logarithm of depth in the light-limited region of the euphotic zone (Fig. 3). Compensation depths estimated from the regression lines fit to the data were also log-normally distributed and in all cases deeper than the compensation depths estimated from the difference between the light bottle and dark bottle uptake (Fig. 2B). The difference between the two sets of compensation depths was significant by a nonparametric sign test at $p = 3 \times 10^{-5}$. The median and geometric mean compensation depths estimated from the 24-h light bottle uptake were 175 and 174 m, respectively.

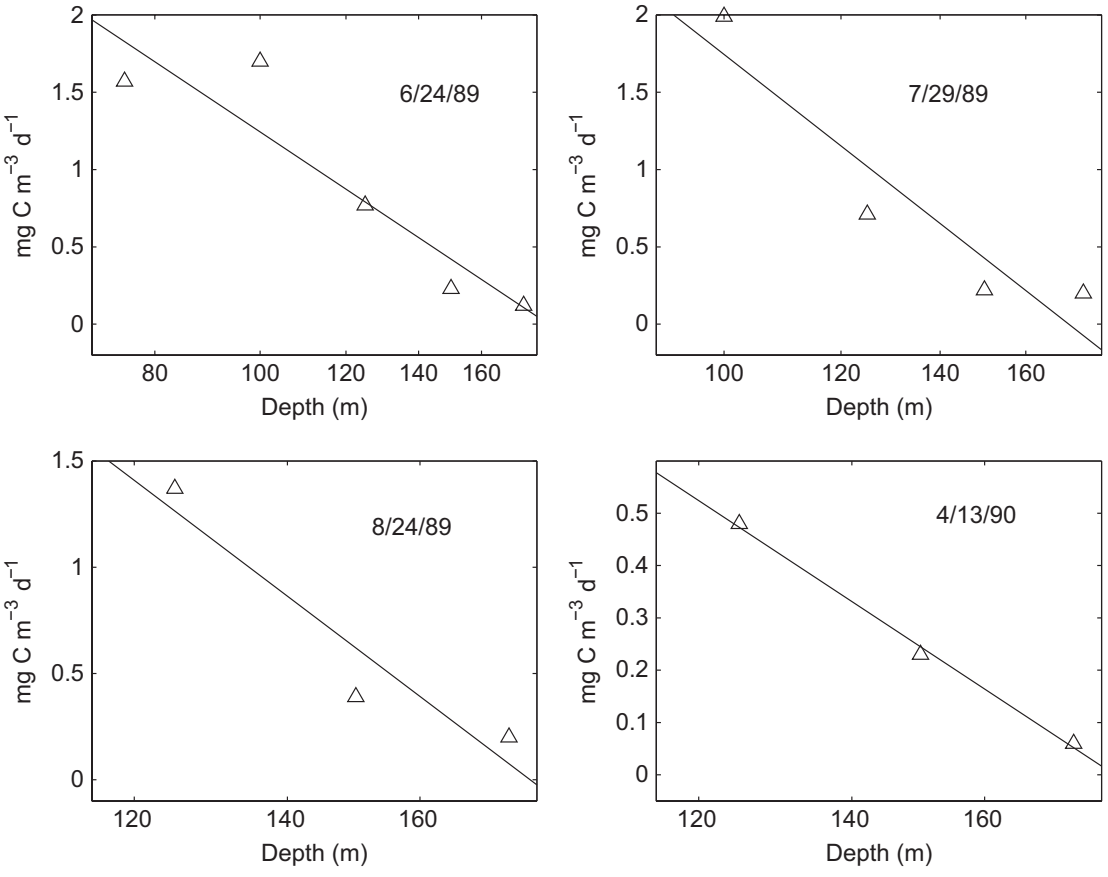


Fig. 3. Graphs of 24-h CO_2 uptake in light bottles versus the logarithm of depth in the light-limited region of the euphotic zone on the same 4 cruises shown in Fig. 1. The straight lines are model I least squares regressions fit to the data.

The natural logarithm of submarine irradiance at station ALOHA was very well described as a linear function of depths greater than 75 m (Fig. 4). The extinction coefficient estimated from a straight line fit to the data was 0.042 m^{-1}, with a 95% confidence interval of 0.038–0.046 m^{-1}. The nonlinearity of the data at shallower depths reflects primarily the preferential absorption of PAR at wavelengths longer than 475 nm. More than half the PAR at wavelengths longer than 600 nm, for example, is absorbed in the first 5 m of the water column. A small percentage (~5%) of PAR is reflected at the sea surface (Jerlov, 1968). Based on the linear regression in Fig. 4, the compensation depths in Fig. 2A and B correspond to irradiances equal to 0.11% (95% confidence interval: 0.06–0.205%) and 0.06% (95% confidence interval: 0.04–0.10%) of surface irradiance, respectively.

To estimate compensation irradiances, we used the daily PAR values at the surface on each sampling day, the corresponding compensation depths (Fig. 1), and the linear regression of the logarithm of depth versus irradiance in Fig. 4. The calculated compensation irradiances were log-normally distributed (Fig. 5). When the compensation depths were estimated from the difference between ^{14}C uptake in light and dark bottles (Fig. 5A), the geometric mean I_C was 0.054 mol-photons $m^{-2}\,d^{-1}$ (95% confidence interval: 0.016–0.178 mol-photons $m^{-2}\,d^{-1}$). When the compensation depths were estimated from ^{14}C uptake in light bottles (Fig. 5B), the geometric mean I_C was 0.025 mol-photons $m^{-2}\,d^{-1}$ (95% confidence interval: 0.010–0.063 mol-photons $m^{-2}\,d^{-1}$). The difference between the two sets of I_C values was significant by a nonparametric sign test at $p=3\times10^{-5}$.

4. Discussion

Most previous information on I_C values has come from laboratory studies on individual species of phytoplankton. The median ($\pm$ median absolute deviation) of such measurements on eight phytoplankton species summarized by Langdon (1988) is 0.20 ± 0.12 mol photons $m^{-2}\,d^{-1}$. These estimates, however, have been based on growth in more-or-less white light (e.g., daylight fluorescent or cool-white fluorescent lamps), and submarine light at the compensation depth is dominated by wavelengths in the blue portion of the visible spectrum, roughly 455–495 nm. Laws et al. (1990) have pointed out that there is a much better match between the spectral characteristics of submarine light in the lower portion of the euphotic zone and the absorption characteristics of phytoplankton accessory pigments such as β-carotene and fucoxanthin than is the case for white light. At 26°N, 155°W they found that the chlorophyll *a*-specific absorption coefficient of marine phytoplankton increased by a factor of 3–4 between the surface and the lower 75% of the euphotic zone. Thus, in terms of the photosynthetically useable radiation (Laws et al., 2002; Morel, 1978; Morel et al., 1996), 0.20 ± 0.12 mol-photons $m^{-2}\,d^{-1}$ of white light is equivalent to roughly 0.057 ± 0.035 mol-photons $m^{-2}\,d^{-1}$ of blue light. Our estimate of 0.054 mol-photons $m^{-2}\,d^{-1}$ for I_C therefore seems very consistent with the results of these earlier laboratory studies.

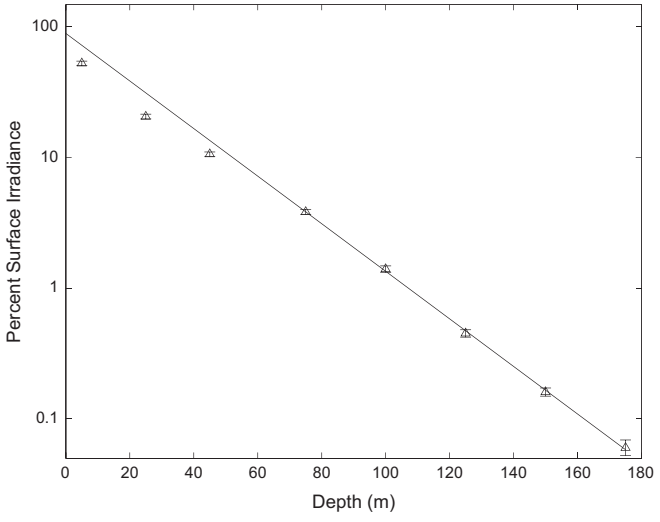


Fig. 4. Submarine PAR as a percentage of surface PAR versus depth from HOT cruises 90 through 147. Error bars are 95% confidence intervals to the mean values at each depth. The straight line is a linear regression fit to the data from 100 m to 175 m.

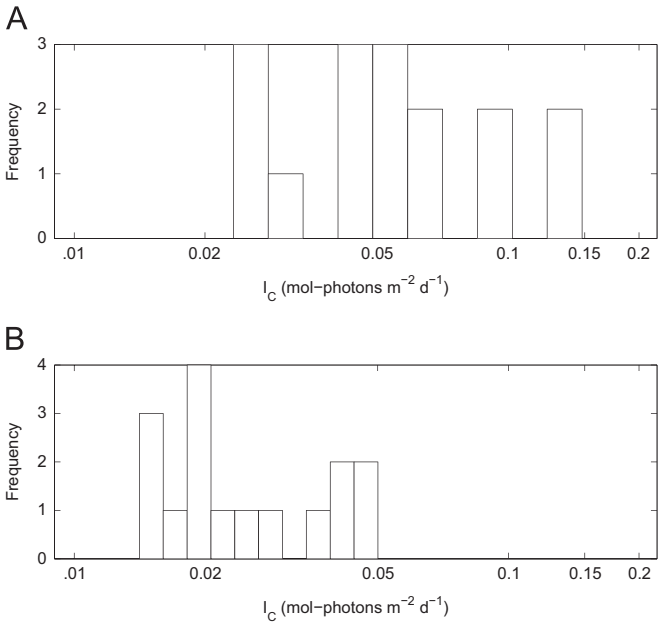


Fig. 5. Histograms of compensation irradiances estimated from the compensation depths in Fig. 2, the linear regression of the logarithm of PAR versus depth in Fig. 4, and the daily surface PAR on each sampling date.

Because light near the compensation point is dominated by wavelengths in the blue portion of the spectrum, it seems logical to ask what percentage of blue light (rather than PAR) is associated with the compensation point (Marra et al., 2014). For type IA and IB seawater, the transmission coefficient of 475-nm light is about 0.97 m^{-1}, (Jerlov, 1968) and for such a light the 1% light level occurs at a depth of 154 m, very similar to the compensation depth at station ALOHA.

Marra et al. (2014) have recently estimated I_C in the western North Atlantic during July in a way similar to the methods we used, but by extrapolating 24-h light bottle ^{14}C uptake rates versus optical depth to zero rather than the difference between light bottle and dark bottle uptake. Their estimated values of I_C averaged 0.17 ± 0.09 mol-photons $m^{-2}\,d^{-1}$. We feel that their calculated I_C values are underestimates of the true I_C values because they failed to account for the non-photosynthetic uptake of ^{14}C at the compensation point. Had we carried out our calculations in a similar manner, our estimate of I_C would have been smaller by a factor of 2, and our estimate of the compensation depth would have been increased by 16–19 m.

The fact that our estimate of I_C is much lower than the estimate of Marra et al. (2014) may reflect differences in the species composition of the phytoplankton communities at the two sites. Even excluding two high I_C values of 2.6 and 3.0 mol photons $m^{-2}\,d^{-1}$ for two dinoflagellates, the I_C values for individual species reported by Langdon (1988) vary by more than an order of magnitude, from 0.065 to 0.78 mol photons $m^{-2}\,d^{-1}$. Temperature is another

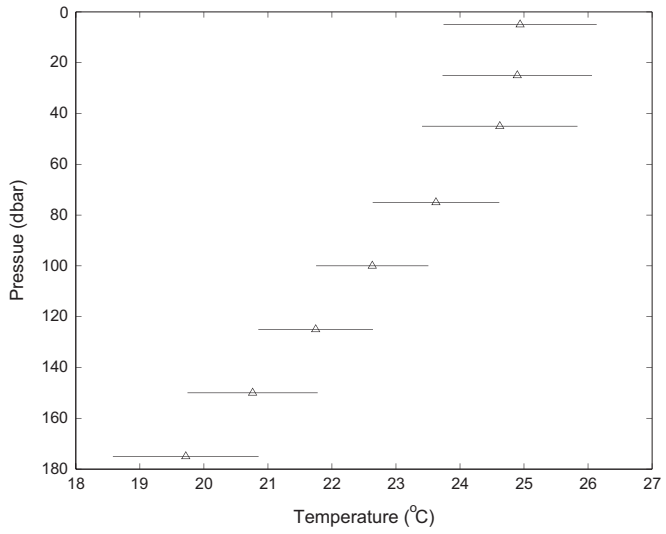


Fig. 6. Average temperatures as a function of depth at station ALOHA. Values are means from CTD casts during HOT cruises 1–248. Error bars are standard deviations.

consideration. Respiration rates are positively correlated with temperature, and the photosynthetic rates required to balance respiratory losses are therefore positively correlated with temperature. Hence compensation irradiances are positively correlated with temperature (e.g., Wieland and Kuhl, 2000). Temperatures at station ALOHA vary from an average of about 25 °C near the surface to <21 °C at depths of 150–175 m (Fig. 6). The in situ incubations of Marra et al. (2014) were carried out during July in the North Atlantic Subtropical Gyre off the east coast of the United States, and the average of the estimated compensation depths was 74 m. Reference to the World Ocean Atlas (NOAA, 2009) indicates that during July in the area sampled by Marra et al. (2014), temperatures at a depth of 74 m would be 18–20 °C. Thus temperature effects do not explain the difference between the two sets of I_C values.

Although both our results and those of Marra et al. (2014) indicate that the compensation depth occurs well below the 1% light level traditionally associated with the base of the euphotic zone, this conclusion should not be extrapolated to cases where the surface irradiance is substantially less than roughly 20 mol-photons m^{-2} d^{-1} (Banse, 2004). Rather than assuming that the irradiance at the compensation depth is a fixed percentage of surface irradiance, it seems more logical to assume that the irradiance at the compensation depth is positively correlated with temperature (Wieland and Kuhl, 2000) but more-or-less independent of surface PAR.

Dore and Karl (1996a) have estimated chemolithoautotrophic (ammonia oxidation) carbon uptake at station ALOHA in water samples collected from depths ranging from 106 to 175 m and subsequently incubated in the dark for 24 h. Their estimated rates of chemolithoautotrophic carbon fixation at depths between 152 and 175 m averaged 95 μg C m^{-3} d^{-1}, which is 48% of the rates of dark carbon fixation (199 ± 43 μg C m^{-3} d^{-1}) that we estimate at depths corresponding to 0.06% and 0.17% of PAR (Fig. 5), i.e., depths of 175 and 150 m. During studies carried out between September 1989 and November 1993, Dore and Karl (1996b) consistently observed primary and secondary nitrite maxima near the base of the euphotic zone at station ALOHA. They attributed the shallower, primary peak to incomplete reduction of nitrate by phytoplankton and the deeper, secondary peak to ammonia oxidation. The average depth of the secondary peak was 149 ± 15 m and is therefore very consistent with chemolithoautotrophic carbon fixation in the depth range 150–175 m.

Species of both bacteria and archaea are known to mediate ammonia oxidation, although rates of ammonia oxidation by these organisms may be temporarily inhibited by exposure to light in the upper water column. However, Dore et al. (1998) have reported evidence of nitrification in near-surface waters at station ALOHA, and Merbt et al. (2012) have reported no evidence of photoinhibition of bacterial ammonia oxidation at an irradiance of 15 μmol photons m^{-2} s^{-1}. At station ALOHA, the average irradiances at depths of 150 and 175 m are 1.7 and 0.6 μmol photons m^{-2} s^{-1}. Although Merbt et al. (2012) found evidence of photoinhibition of ammonia oxidation by archaea at 15 μmol photons m^{-2} s^{-1}, there have been no reports of photoinhibition of ammonia oxidation by archaea at light levels of 1.7 μmol photons m^{-2} s^{-1} or lower. It therefore seems likely that roughly half of the ^{14}C uptake at 150 and 175 m at station ALOHA is due to the activities of ammonia-oxidizing microorganisms or other chemolithoautotrohpic processes. The remainder of the CO_2 uptake in light bottles at those depths may reflect nothing more than anaplerotic CO_2 uptake by autotrophic and heterotrophic organisms. However, if phytoplankton respiration rates exceed gross photosynthetic rates, it is axiomatic that some of the carbon respired by phytoplankton is old carbon. In that case, ^{14}C uptake will clearly be an overestimate of net photosynthesis, even after correction for non-photosynthetic uptake. If the dark-bottle-corrected ^{14}C uptake rate is simply zero, as is the case in our results (Fig. 1), the implication is that all ^{14}C taken up is respired and escapes from the cell, or that the gross uptake of ^{14}C is zero at irradiances lower than I_C, and that respiratory demands are met entirely by catabolizing old carbon.

A final point concerns the concept of the compensation depth: the existence of a compensation depth implicitly assumes that phytoplankton remain at a fixed depth throughout a 24-h period. At station ALOHA, however, vertical displacements of isopycnals over distances of tens of meters can occur on a timeframe of hours at depths of 100–150 m (Karl et al., 2002). The effects of such vertical excursions on integral production will be nonlinear to the extent that the excursions extend outside the range of depths within which photosynthesis and depth are linearly related, e.g., outside the depth range ~100–150 m at station ALOHA. Under such conditions, there is no depth in the water column that can be identified as the compensation depth. Instead, the compensation depth is the depth at which net photosynthesis would be zero over 24 h in the absence of vertical movement in the vicinity of the compensation depth.

5. Conclusions

The compensation irradiance at station ALOHA equals 0.054 mol-photons m^{-2} d^{-1}, which corresponds to 0.11% of surface PAR and about 1% of surface 475-nm light. The uptake of inorganic carbon calculated from ^{14}C uptake in bottles containing water from the depth corresponding to this irradiance is not zero, but instead averages 199 ± 43 μg C m^{-3} d^{-1}. About half of that uptake can be attributed to chemolithoautotrohphy. The remainder is presumably due to anaplerotic processes. Accurate estimation of the compensation irradiance based on ^{14}C tracer studies requires that allowance be made for non-photosynthetic uptake of CO_2. At station ALOHA, ignoring non-photosynthetic CO_2 uptake results in underestimation of the compensation irradiance by about a factor of 2.

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